



Article Investigation of the Secondary Succession of Abandoned Areas from Different Cultivation in the Pannonian Biogeographic Region

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Abstract: Areas abandoned for various reasons are widespread on Earth, with a significant proportion in some regions of Europe. Our knowledge of vegetation dynamics in abandoned lands is incomplete, in part because research comparing types abandoned from different cultivars is limited. This paper compared the textural and structural changes of previously extensively treated vineyards, arables, and grasslands over a 30-year timescale in secondary succession studies. Based on the botanical surveys, it can be said that the total species number and diversity of abandoned vineyards and arable lands did not increase linearly in the four age groups studied. The way of secondary succession of former vineyards and arable lands showed many similarities. In these types, rapid regeneration of natural vegetation can be observed, the rate of which can only be reduced by the abundance of a few strong competitor species. However, the abandonment of extensively grazed and mowed grasslands has reduced species numbers and diversity, which may reduce the resilience of such grasslands to environmental factors. In abandoned lands, the mosaic landscape and previous extensive small-plot farming appear to have a positive effect on the rate of secondary succession and regeneration, as the species-rich vegetation patches provide a suitable propagule source for regeneration.

Keywords: space for time; chronosequence; vineyards; arables; pastures; hayfields; species richness; diversity indices; naturalness; Raunkiaer life forms

1. Introduction

The traditional landscape has changed significantly in many European countries in recent decades [1,2]. On the site of previously agricultural areas, abandoned lands are found in several regions [3–5]. Factors leading to landscape abandonment may include environmental (e.g., reduced soil ferility, degradation caused by overgrazing) or socio-economic causes (depopulation of the rural area in remote regions, socio-political changes) [6]. A CORINE-based study showed that the highest rate of abandonment of arable land occurs in East Central Europe, Ireland, and Southern Europe during the period 1990–2006 [3]. In East Central and Southern Europe, abandonment happened more in undulating terrain with shallow soils. In addition to arable land, the abandonment of vineyards and grasslands is also significant; for example, the vineyard area in European countries is declined by over 6% between 1999 and 2009 [2]. Moreover, in many highlands of Europe, the abandonment of traditional mowing cultivation is common [7].

Secondary vegetation has developed in the abandoned areas, providing an excellent basis for various spontaneous secondary succession studies [5,8–11]. The space-for-time



Citation: Szirmai, O.; Saláta, D.; Benedek, L.K.; Czóbel, S. Investigation of the Secondary Succession of Abandoned Areas from Different Cultivation in the Pannonian Biogeographic Region. *Agronomy* **2022**, *12*, 773. https:// doi.org/10.3390/agronomy12040773

Academic Editor: Junhu Dai

Received: 10 February 2022 Accepted: 19 March 2022 Published: 23 March 2022

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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). substitution or chronosequence method—e.g., Refs. [12,13]—has been widely used to study long-term vegetation dynamics.

As in other parts of Europe, the number of abandoned areas in Hungary has increased in recent decades, mainly due to socio-economic, rural depopulation, globalization, and agrarian financing. The most abandoned areas (7.8%) are located in the North Hungarian Mountains [14]. The latter region has traditionally been characterized by peasant farming, and the outskirts of the villages were mainly covered with extensive vineyards, arable land, hayfields, and pastures. Today, however, the proportion of cultivated land has decreased significantly in several regions, such as the Tardonai Hills [15]. The Tardonai Hills and several surrounding microregions are largely covered by vegetation of abandoned lands from various cultivation methods [16,17], which also provide an excellent basis for conducting secondary succession studies and comparing results [18].

In Europe, conventional grazing has a positive effect on the species richness of vegetation, especially on continuously, long-term mowed and grazed grasslands, and is well tolerated by rare or endangered species [7,19–25]. Some research to date shows that the species richness of grasslands decreased after the abandonment of grazing [18,26–28] but this was not the case for rare species [28]. Other researchers, on the other hand, have found that abandonment has not changed or even increased species richness [22,29,30]. The differences are due to the fact that, in addition to the grazing rate, environmental factors also affect the species richness; grazing has a species-number-increasing effect in addition to productive site factors, but species richness decreases in low productivity, dry sites [20,31,32].

Different results have also been published on the effect of grazing for diversity. Several studies found a decrease in species diversity with land-use abandonment—e.g., Refs. [33–36]—while others found no or minor difference—e.g., Refs. [35–37]. Even within a region, the diversity of former hayfields and pastures changed variably [38]. Abandonment of hayfields changed the species pool, which ultimately leads to a decline in species diversity [39]. The decline in the number and diversity of grasslands is, in many cases, the result of the increasing dominance of strong competing species associated with a given community [40]. In addition, plant diversity can be more strongly affected by other factors, such as the biogeographic species pool, land-use history, type of management, or processes such as bush encroachment [18].

The previous utilization method (pasture or hayfields) influences the distribution of abandoned grassland life forms; as the cover of annuals and biennials in a sheep pasture decreased minimally after abandonment, they conversely increased in former hayfields [38]. Other results have shown an increase in the proportion of annuals in abandoned areas [38,41–43] and found that hemicryptophytes were dominant throughout, while the number and cover of perennial taxa has increased in both abandoned pastures and hayfields [44], including herbaceous dicots taxa and large perennial grasses [30]. The latter may be justified by the fact that grazing reduces the cover of tall grasses and dicots [45]. The cover of geophytes has increased on the abandoned hayfields, while it is stagnant on the unused pastures [38]. Interestingly, the cover of dwarf shrubs (Ch) decreased more strongly on the abandoned hayfields than on the pasture fallow [38]. Contrary to the former, the cover of dwarf shrubs also decreased in intensively grazed areas [46]. Coverage of tree life forms increased on pasture fallow; however, they were not present on the abandoned hayfields [38]. In intensively grazed areas, prickly shrubs may become dominant according to Chen et al. [30].

As stated by the naturalness study of abandoned grassland species, the cover of competitors in the abandoned sheep pasture and meadow increased, while the cover of ruderal competitors increased in the meadow and decreased in the pasture. Coverage of stress tolerants decreased in the meadow and doubled in the pasture [38].

Regarding the changes in the species richness of abandoned arable lands, several studies have shown that the total species richness increased in the examined succession period and in the patch scale, and stabilized later [47,48]. Contrary to previous observations,

early succession studies showed that species richness was highest in the first year after abandonment, and then decreased significantly over the next 3 years of the study [49] or showed a broadly declining trend, nonlinear change, and no clear trend as succession progressed [1,50,51]. The succession of abandoned lands was initially greatly influenced by the date of abandonment, the type of last crop before abandonment, and its weed vegetation, landscape history, soil water supply, and organic carbon content [51–54].

The vegetation diversity of abandoned arable land generally increases during succession [47,48,55,56]. Somewhat contrary to the previous case, in other observations, the diversity in younger abandonments increased (between 4 and 11 years), and then decreased [50]. Some studies show that the decrease occurred later (after 20 years) [57,58]. In contrast to Molnár and Botta-Dukát [50], the initial low diversity only increased in the second year and remained stable for the other two years studied [49]. Diversity was maximal in the period dominated by annual taxa, and then decreased with their disappearance, but, when perennial dicots were replaced by perennial grasses, it was high again, and then showed a decrease again [59].

During old-field succession, a so-called dominance sequence was observed for lifestyle types. The first stage was dominated by annuals, then biennials, then perennials, and, finally, woody ones [57,60–63]. In contrast, some researchers have found that perennial species of natural grasslands and other dicot and woody taxa were able to settle in the first years [64]. Although the number of weeds decreases as a function of the time elapsed since abandonment [48], the lifespan of annual weeds may vary, with a sudden decrease after abandonment [18]. In some cases, annuals or weeds may dominate an area for several years [1,50]. The number of dicots was also the highest in the first 10 years, and then more or less declining [1]. The number of species of grasses showed an increasing trend in the first 10 years, and their cover increased sharply from the 11th and the 15th year [1,50]. The number of woody species increased exponentially, but their cover showed a linear upward trend [1].

Regarding the naturalness of old-field species, it can be said that, if semi-natural vegetation is not present in the vicinity of the abandoned arable, only generalist species appear predominantly [50,65–68]. Weeds were low on 5–14-year-old and almost nonexistant on 20-year-old fields. The number of weeds and alien species decreases as a function of time since abandonment, while the number of natural and semi-natural habitat species increased Ruprecht [48].

In abandoned vineyards, some experience has shown that species richness decreased as succession progressed [58,69], and species density increased more significantly after 10 years [2]. Seedlings of tree and shrub life species settle in abandoned vineyards in the early stages of succession and their number increases over time [2,58,69,70]. The number of therophytes decreases, but may even disappear [58,69–71]. Alternatively, others revealed the persistence of annual grasslands throughout the abandonment pathway, and even annuals dominate in the first few years [2,72,73]. The perennial hemicryptophytes (H) and chamaephytas (Ch) appeared from year 3 [2]. Ne'eman and Izhaki [70] observed that all perennials survived in the fallow. After the first few years of the secondary succession process, perennial tall grasses may appear in the vegetation of certain abandoned vineyards and may even become abundant [71,73]. In some cases, dominance of hemicryptophytes (51.38%) was observed even in the vegetation of vineyards under extensive cultivation, followed by therophytes (34.86%) [74].

There is relatively little literature on the naturalness of abandoned vineyard species. Ruderal species have been recorded in an abandoned and herbicide-free plot for 2 years as early as the year of the study [74]. In the Putnoki Hills, close to the object of the present research (Tardonai Hills), it has been found that the abandoned vineyards of 1–40 years old are dominated by generalist species, suggesting natural conditions [17]. These are followed by natural disturbance-tolerant (DT) species, with a value of around 30%. The proportion of weed species was 9%, but, fortunately, the proportion of adventive species (A) did not

reach 1%. According to the SBT categories, the proportion of ruderal and alien competitors (RC, AC) is almost the same (approx. 8–8%).

According to the landscape history records, prosperous traditional small-scale peasant farms characterized the Tardona Hills from the end of 18th century to the mid 20th century. However, after the Second World War, due to depopulation processes, negative age distribution, and industrialization, the number of arable lands was strongly decreased. After the Second World War, vineyards enlarged a little but, since 1984, a growing number of abandoned areas have been observed everywhere on the ridge [15]. These areas have since been populated by different vegetation patches at various succession stages. The floristic and coenological results from various vegetation belts are determined by exposure, abandonment, and former cultivation regime, and they can provide a good base for subsequent vegetation investigations [75]. A quarter of the research area is covered by natural and semi-natural forests, and more than half by regenerating vegetation of areas abandoned from different cultivation. This cultivation is interspersed with refuge areas rich in forest steppe species [76,77]. Semi-natural grass patches are mainly classified as Festuco–Brometea (within that, mainly Festucetalia valesiacae and Brometalia erecti orders). Of the 10 forest types, the most significant are the shares of *Quercetum petraeae–cerris* (43% of forests) and Carici pilosae-Carpinetum (33% of forests). The proportion of forest patches formed by alien tree species is relatively low (*Robinia* forest 8.6%), with *Picea abies* and *Pinus* sylvestris plantations and mixed foliage plantations both 1.7% compared to the total forest area [77].

In the course of the research, we examined the secondary succession of abandoned areas with different land-use histories (vineyards, arable land, hayfields/pastures) in four different age groups in the same landscape using the 'space for time' method.

The following questions were addressed:

- (1) How does the total species richness and diversity of abandoned land vary by former cultivation type and age group?
- (2) What differences and tendencies can be detected in the examined fallow types in the case of life forms and naturalness (SBT) during abandonment?
- (3) Based on their species composition and dominance relations, what groups can the selected abandoned lands be classified into?

2. Materials and Methods

2.1. Study Site

The location of the research was about a 4 km² area of the Tardonai Hills in the northeastern part of the Bükk Mountains in northeastern Hungary (Figure 1). The studied area belongs to Sajókápolna [76]. Mainly since the 1980s, more and more plots have been abandoned in the selected area, which was also typical of other regions in northern Hungary [14]. The average temperature of the area is 9 °C and the average annual rainfall is 600 mm [75]. The elevated plots ranged in height from 180 to 280 m and ranged in size from 0.15 ha to 1 ha. Predominantly brown forest soils were formed on clay sediments, Pannonian sand, and their crumbs mixed mainly with rhyolite tuff [15].

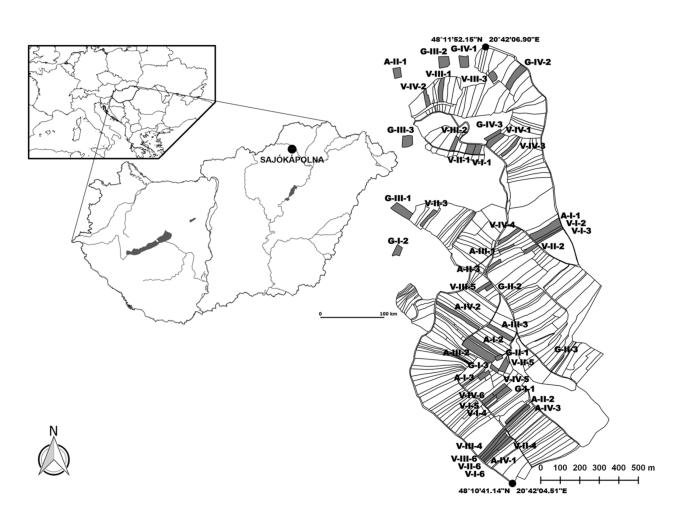


Figure 1. Location of the study site and studied plots—based on a cadastral map (1971) and fieldwork (The inicial letters indicate the type of abandonment: V—vineyards, A—arable land, G—grasslands; the middle latin numbers indicate the period of abandonment I: 1–5 years, II: 6–10 years, III: 11–20 years, IV: 21–30 years; the last Arabic numbers indicate the plots examined; the arrow shows North).

2.2. Botanical Sampling

In the framework of secondary succession studies, botanical samplings were carried out on abandoned plots of different cultivation types, such as vineyards, arable lands, pastures, and hayfields (the latter two are collectively called grassland type due to their similar nature). From the date of abandonment, the plots were divided into the following four age groups: age group 1 (abandoned 1–5 years), age group 2 (abandoned 6–10 years), age group 3 (abandoned 11–20 years), and age group 4 (abandoned 21–30 years ago). In this way, so-called chronological sequences were created, which formed the basis of the spacefor-time substitution study. A minimum of 3–3 plots were botanically recorded for each abandonment type and age group. During the botanical surveys in each plot, a minimum of 5 coenological samples were carried out between 2001 and 2021. The sampling sizes were $2 \text{ m} \times 2 \text{ m}$, and squares were arranged randomly within the plot. During the sampling, a total of 254 squares of vegetation were covered (covering a total of 1016 m²), based on the estimation of the percentage cover values of all vascular plant species occurring within the square. We used a cadastral map (1971, 2000), topographic map (1984), and aerial photographs (1990, 2000) to determine the age of the abandoned lands, and we also collected information from local farmers about each abandoned land. The latter has been validated by maps and aerial photographs.

2.3. Data Evaluation

The vegetation of different abandoned lands was evaluated on the basis of textural and ecological characteristics of the species' (social behavior types, life forms) averaged cover (Appendix A, Table A1). Shannon and Simpson indices were used to calculate diversity. To characterize the succession stages, we used the coenogroups of the taxa in the recordings [78], Raunkiaer's life forms [79] based on Simon's [80] work, and Borhidi's naturalness category or so-called social behavior types (SBT) [76,78]. The social behavior types (SBT) are integral parts of the competitor, stress tolerator, ruderal (C–S–R) strategic model of Grime [81]. SBT types are the following: competitors (C), stress tolerants (ST) of narrow ecology: specialists (S), and stress tolerants (ST) of wide ecology: generalists (G). Ruderals (R) include the following categories: natural pioneers (NP), disturbance-tolerant plants of natural habitats (DT), native weed species (W), introduced alien species (I), adventitives (A), ruderal competitors (RC), alien competitors, and aggressive invadors (AC) [78].

The nomenclature of species follows the work of Simon [82] and that of coenotaxons in Borhidi and Sánta [83].

2.4. Statistical Analysis

The data were processed using two-sample Mann–Whitney test (two-tailed U test to test samples for difference) [84], alpha diversity module [85] (Shannon and Simpson as most commonly used indexes to identify changes in diversity due to the abandonment), diversity permutation test [86] (comparison of samples diversities using random permutations to highlight differences), and PCA multivariate analysis [87] (principal component analysis for better understanding of the inner structure of data) of the PAST (PAleontological STatistics Version 4.08, Oslo, Norway) statistical software package [86,88]—the values obtained are expressed with 4 decimals, except for justified cases. To visualize the results, PAST, QGIS 3.16.12 'Hannover', Excel, and PowerPoint (Microsoft Office Professional Plus 2016, Gödöllő, Hungary) software packages were used.

3. Results

3.1. Species Richness

A total of 243 vascular plant species were recorded in the 254 sampling squares. Of the former, 156 species were included in the surveys of abandoned vineyards, 138 in abandoned arable land, and 166 in abandoned grasslands. Of the listed species, five are protected in Hungary and four are on the IUCN Red List [89].

As time elapsed since abandonment, the total species richness for both vineyards and arable land increased steadily over the study period (Figure 2). There is a smaller but statistically significant difference (p < 0.05) in the total species richness of abandoned vineyards between age groups 1 and 2, and 2 and 4, while there is a strong significant difference (p < 0.001) in age group 1 and between the third and fourth age groups (Table 1). In the case of vineyards, the growth rate was almost uniform between age groups and the species number value after abandonment (47 species) more than doubled in the oldest age group (97 species).

In the case of arable land, the increase in the total number of species was slightly smaller compared to vineyards during the study period, but the initial total species richness (50 species) almost doubled in two decades (92 species). In the abandoned old-fields, the increase in the total number of species was less uniform than in the case of the vineyards. This is because the increase in the total number of species were found between age groups 1 and 3 (p < 0.05), 1 and 4 (p < 0.001), and 2 and 4 (p < 0.05) (Table 1).

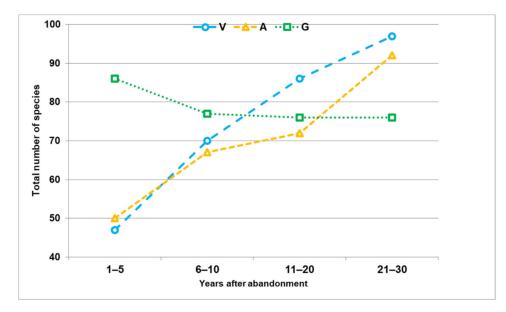


Figure 2. Changes in the total number of species in the studied age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

Table 1. Statistical results of the total species richness of abandoned land types for the studied age groups (V—vineyards, A—arable land, G—grasslands).

	Mann–Whitney Test Results													
V/1-5-V/6-10 A/1-5-A/6-10 G/1-5-G/6-									/6–1	0				
Z	2.5062	р	0.0122	z	1.7434	р	0.0812	Z	0.84747	р	0.3967			
	V/1-5-V	/11–2	0		A/1-5-A	/11-	G/1-5-G/11-20				20			
Z	4.0561	р	0.00004	z	2.3983	р	0.0164	Z	1.4063	р	0.1596			
	V/1-5-V	/21–3	0		A/1-5-A	/21-	30		G/1–5–G/	/21–3	30			
Z	5.0903	р	0.000000	3 z	4.0292	р	0.00005	Z	0.92189	р	0.3565			
	V/6-10-V	//11-2	20		A/6–10–A	/11-	-20		G/6–10–G	/11-	20			
Z	1.5430	р	0.1228	z	0.65213	р	0.5143	Z	0.51588	р	0.6059			
	V/6-10-V	/21-3	30		A/6–10–A	/21-	-30		G/6–10–G	/21-	30			
Z	2.5636	р	0.0103	z	2.3033	р	0.0212	Z	0.056086	р	0.9552			
	V/11-20-V	//21-	30		A/11-20-A	A/21-	-30		G/11-20-G	/21-	-30			
Z	1.0692	р	0.2850	Z	1.582	р	0.1136	Z	0.43951	р	0.6602			

In the case of former pastures and hayfields, a larger decrease in the total number of species can be seen in the first 10 years, followed by a much smaller decrease in the number of species in the following decades (Figure 2). The number of species of the youngest abandoned land (86 species) decreased to 76 species in the case of the oldest fallow studied, i.e., the rate of reduction in the total number of species was slightly higher than 10%.

3.2. Diversity Indices

In abandoned grapes, both Shannon and Simpson diversity values increased steadily after abandonment (Figure 3). The value of Shannon diversity in the first period after abandonment more than doubled from 1.39 to 2.93. Significantly higher increases in the diversity were obtained in the youngest abandoned vineyards (1–5 years) and other age groups (p < 0.001), including age groups 2 and 4 (p < 0.001), and age groups 3 and 4 (p < 0.001) when examining Shannon diversity (Table 2). For Simpson diversity, there was a significant difference between age groups 1 and 3 (p < 0.05), age groups 1 and 4 (p < 0.01), and age groups 2 and 4 (p < 0.05) (Table 2).

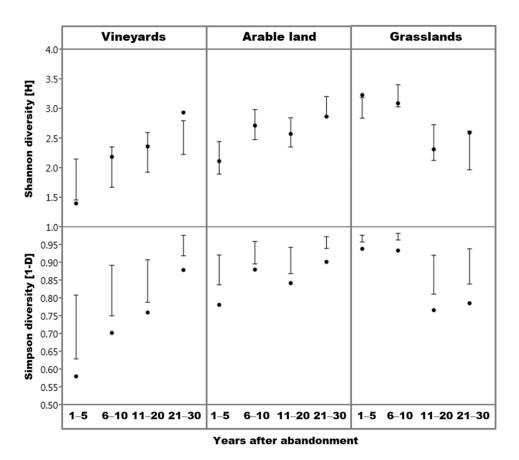


Figure 3. Changes in Shannon and Simpson diversity values in age groups of abandoned lands (PAST 4.08 uses 1-D formula for Simpson index [86]).

Table 2. Statistical results of the diversity of abandoned land types for the studied age groups.

	Diversity Permutation Test Results—Perm <i>p</i> (eq)													
	-V/6–10		A/1-5-	-A/6–10		G/1-5-G/6-10								
Shannon	0.0002	Simpson	0.4359	Shannon	0.0003	Simpson	0.0001	Shannon	0.1142	Simpson	0.7686			
	V/1-5-	V/11-20			A/1-5-	A/11-20			G/1-5-	G/11–20				
Shannon	0.0001	Simpson	0.0392	Shannon	0.0037	Simpson	0.0044	Shannon	0.0001	Simpson	0.0001			
	V/1-5-	V/21-30			A/1-5-	A/21-30		G/1-5-G/21-30						
Shannon	0.0001	Simpson	0.0011	Shannon	0.0001	Simpson	0.0001	Shannon	0.0049	Simpson	0.0001			
	V/6-10-	-V/11–20			A/6-10-	-A/11–20								
Shannon	0.5779	Simpson	0.2403	Shannon	0.5244	Simpson	0.2163	Shannon	0.0001	Simpson	0.0001			
	V/6-10-	-V/21–30			A/6-10-	-A/21-30			G/6–10-	-G/21-30				
Shannon	0.0003	Simpson	0.0189	Shannon	0.3497	Simpson	0.3940	Shannon	0.0264	Simpson	0.0001			
	V/11-20	-V/21-30			A/11-20	-A/21-30			G/11-20-G/21-30					
Shannon	0.0002	Simpson	0.1701	Shannon	0.0903	Simpson	0.0171	Shannon	0.0603	Simpson	0.6906			

In the case of arable land, the pattern of the two diversities was also the same, the diversity values were the lowest for the youngest old-fields, and the highest for the oldest old-fields. In the intervening periods, the break in the steady increase in diversity occurred in the second decade after abandonment, when both indices showed a slight decline. In arable land, the significance levels of Shannon and Simpson diversity were similar in 1 and 2 (p < 0.001), 1 and 3 (p < 0.01), and 1 and 4 (p < 0.001) age groups, and Simpson diversity showed a significant increase between age groups 3 and 4 (p < 0.05) (Table 2).

In abandoned hayfields and pastures, diversity decreased in the initial period and then increased again after 20 years. The lowest diversity values were for the 11–20-year parcels and the highest for the 1–5-year parcels for both diversity indices. On abandoned meadows and pastures, Shannon and Simpson diversity indicate similar significance level decreases between age groups 1 and 3 (p < 0.001), 2, and 4 (p < 0.001) (Table 2). There was also a significant difference between age groups 1 and 4 (Shannon p < 0.01, Simpson p < 0.001) and age groups 2 and 4 (Shannon p < 0.05, Simpson p < 0.001).

In the case of abandoned lands, the initial (age group 1) Shannon diversity values were 1.39, 2.11, and 3.23 for vineyards, arables, and grasslands, respectively. After about 30 years (age group 4), these diversity values change to 2.92, 2.86, and 2.59 for vineyards, arables, and grasslands, respectively.

3.3. Naturalness

In vineyards, the cover value of ruderal competitors (RC) was the highest among the categories in the first 10 years, but, similarly to the introduced alien species (I), its proportion continuously decreased after abandonment (Figure 4). The proportion of competitors (C) and generalists (G) has increased, with the latter already dominating 21- to 30-year-old abandoned lands. Sensitive specialists (S) appeared 10 years after abandonment. The rate of disturbance tolerance (DT) increased compared to the youngest fallow, and then decreased to a period of 21–30 years. With the former, the share of alien competitors (AC) shows the opposite trend. The proportion of weeds (W) was highest in the 5–10 age group, but, again, only by a few percent. The number of SBT types did not change when examining the youngest and oldest abandoned vineyards.

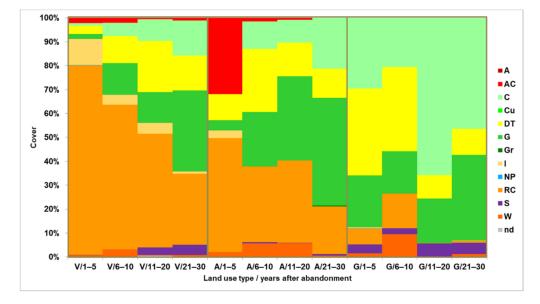


Figure 4. Distribution of naturalness (social behaviour types) in age groups of abandoned lands (A—adventives, AC—alien competitors, C—competitors, Cu—unique competitors, DT—disturbance tolerants, G—generalists, Gr—rare generalists, I—introduced alien species, NP—natural pioneers, RC—ruderal competitors, S—specialist, W—weeds, nd—no data).

In arable land, the share of the initial highest proportion of ruderal competitors (RC) was less than halved after 20 years, while the share of generalist species (G) increased spectacularly (Figure 4). After 5 years, competitors (C) and sensitive specialist species (S) appeared. In the 21–30-year-old age group, the generalist species were already dominant and the ceompetitors were subdominant. The initial high share of alien competitor species (AC) in total cover decreased spectacularly after 5 years, and then these species disappeared from the old-fields after 20 years. The smaller share of introduced alien species (I) had completely disappeared from the old-fields already after 5 years. The proportion of weeds

10 of 22

(W) was highest in the 11–20 age group (5–6%). SBT categories were represented by eight types in the youngest old-fields, but this number increased to 10 for the oldest abandoned lands studied.

In grasslands, the proportion of competitor species (C) increased dramatically after 10 years and even became dominant from the 11th year (Figure 4). In contrast, disturbance tolerances (DT) were greatly reduced. The share of ruderal competitors (RC) in older fallows has become insignificant. It can be seen that the proportion of sensitive specialist species (S) has increased in the two oldest age groups. The proportion of weeds (W), similar to vineyards, was highest in the 5–10-year-old age group. The number of SBT categories has dropped from 10 to 7, ranging from the youngest to the oldest.

3.4. Life Forms

In vineyards, the proportion of the dominant hemicryptophytes (H) life form decreased after 20 years (Figure 5), but remained dominant throughout. The proportion of annual (Th) species decreased significantly after initial growth. The trend of biennial (TH) species is similar to that of annuals (Th), with the difference that the proportion of biennials has increased significantly in the case of the oldest surveyed fallows. The proportion of perennial cryptophyte (G) species has been steadily declining, from a very significant extent from the second decade after abandonment. The ratio of chamaephyte species (Ch) was close to 0 or 0, except for the 11–20-year period, similar to that of woody nanophanerophyte species (N). In the latter, however, the coverage fell to 1 in the 21–30-year interval. Among the woody groups, the proportion of microphanerophytes (M) shows a fluctuating trend, as does the proportion of mesophanerophyte species (MM), but, in the latter group, the changes between age groups are substantially smaller. In vineyards, the number of life forms found in the youngest fallows increased from eight to nine in the oldest abandoned lands.

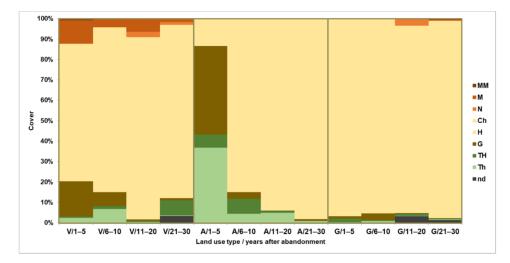


Figure 5. Distribution of Raunkiaer life forms in age groups of abandoned lands (MM— mesophanerophytes, M—microphanerophytes, N—nanophanerophytes, Ch—chamaephytes, H— hemicryptophytes, G—geophytes (cryptophytes), TH—hemitherophytes, Th—therophytes, nd— no data).

In arable land in the immediate post-abandonment period, the proportion of codominant G and Th life form species in the cover was strongly reduced and was minimally present in the over-20 age group (Figure 5). The share of annuals (Th) was highest in age group 1, and then decreased sharply among 6–10-year old-fields. The proportion of biennial (TH) species decreased after the first two age group increases. The coverage rate of hemicryptopyte (H) species increased spectacularly after 5 years and became dominant in the old-field. Among woody types, the proportions of N, M, and MM life forms were close to/equal to 0, while chamaephyte (Ch) species appeared after 20 years in substantial proportions. In arable land, the number of life forms increased from four to seven during the study period.

In the case of abandoned grasslands, the cover rate of the absolutely dominant hemicryptopyte (H) life form species in all age groups decreased for 20 years, and then increased, but did not reach previous levels (Figure 5). The share of annuals (Th) was small in all age groups (with values below 1%), but their share was fluctuated, while that of biennial (TH) species showed a slightly declining trend. The proportion of geophyte species (G) initially increased, and then decreased significantly after 10 years. The proportion of woody chamaephytes (Ch) shows a fluctuating but overall increase, as does that of nanophanerophyte (N) species. The oscillations of the latter group were more significant. The coverage rate of woody types (M and MM) increased after 20 years and did not exceed 0.5%. In abandoned grasslands, the number of life forms increased from seven to nine, observed in the youngest fallows in the oldest abandoned lands.

3.5. Multivariate Analysis

Based on the multivariate analysis, the studied abandoned sites are largely arranged according to the previous cultivation types (Figure 6). The grasslands are well separated, while, in the case of vineyards and arable land, the 1–1 sample area (A/11–20, V/21–30) is located in the other type or further away from the others (A/1–5).

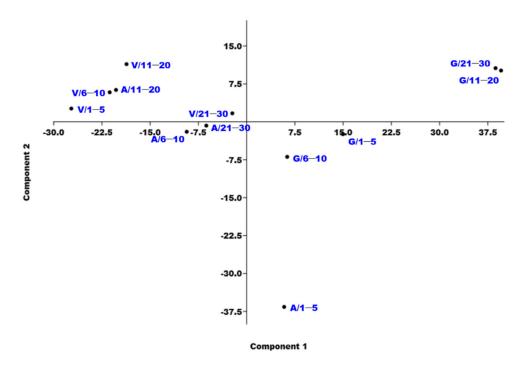


Figure 6. Result of the multivariate PCA analysis (V-vineyards, A-arable land, G-grasslands).

4. Discussion

4.1. Species Richness

In abandoned vineyards, the total number of species increased steadily (Figure 2), in contrast to Debussche et al. [58,69]. The continuous increase in the total species richness after abandonment was facilitated by the fact that the cover values of the mainly monodominant *Calamagrostis epigeios* decreased over time. Following 6–20 years after abandonment, *Calamagrostis epigeios* predominated. Other researchers [90] have also shown that the latter taxon becomes permanently monodominant in older fallows. After 21 years, the cover of *Calamagrostis* has decreased, with *Inula salicina*, *Inula ensifolia*, *Festuca*, and *Thymus pannon-icus* dominating, themore or less closed patches of which *Calamagrostis* no longer really appeared. In the oldest fallows, *Calamagrostis* has already occurred in several squares with low or only scarcely covering values, which favored the more abundant appearance of dry grass or forest steppe species (e.g., Brachypodium rupestre, Inula britannica, I. ensifolia, Stipa pulcherrima, Poa angustifolia, Potentilla alba). This trend has already been observed by other researchers [71,73,90]. The total number of species in the arable land increased continuously during the succession [5,47,48], and the increase in the species richness was less even than in the vineyards. This can be attributed to the small increase in the total number of species being small in the case of 11–20 year olds. An increase in the total species richness in the vegetation of regenerating arable land has been reported by a relatively large number of studies—e.g., Refs. [47,48,56]. Slightly contrary to the former, some researchers have found that the number of species decreases as succession progresses or does not change linearly or similarly with the age of fallows [1,49–51]. In addition to the dominant weed species (e.g., Erigeron annuus, Conyza canadensis, Elymus repens, Cirsium arvense) in the 1-2-year old-fields (mostly former maize or potato fields), species of ruderals and natural grasslands can also be found in the community, such as *Picris hieracioides* and *Libanotis pyrenaica*, among the latter with natural grasses (Koeleria cristata, Festuca rupicola). Due to the small size of the parcels, the more natural species of the former hedges and adjacent areas can colonize the abandoned land more easily, thus accelerating the initial process of secondary succession, similar to the observations of Ruprecht [48,56], Házi and Bartha [90].

During the secondary succession of former pastures and meadows (grasslands), the total number of species initially decreased, and then almost stagnated. The decrease in species richness of abandoned pastures has been confirmed by other researchers [18,26–28]. In contrast, others have observed an increase or stagnation in the number of species in grasslands over time after abandonment [22,29,30]. The abandonment of previous grazing and mowing has a different effect on the species richness and cover of stands with different production sites, environmental needs, species composition, and dynamic status [20,31,32]. In this case, therefore, discontinuation of treatment was initially associated with a reduction in species number and cover; the abundance of some species decreased (e.g., *Arrhenatherum elatius*) and that of other taxa (e.g., *Calamagrostis epigeios*, *Brachypodium rupestre*) increased during succession, as in other studies—e.g., Refs. [40,90,91].

Based on the curve (Figure 2), the number of species was not saturated in either the vineyards or the arable lands, so a further increase in the total number of species is expected for both types, even after 30 years. In the case of grasslands, the total species number of abandoned pastures and meadows appears to be close to equilibrium in 3 decades.

4.2. Diversity Indices

In the case of vineyards, the significant increases in diversity between 6 and 10 years and then after 20 years were found (Figure 3). The former change in diversity values was similar to that of Tatoni and Roche [57] and Debussche et al. [58]. The latter suggests a slower succession of abandoned vineyards and abundance of strong competitor species [40,47] in some age groups. In the 6–20-year-old vineyards, where the abundance of *Calamagrostis* was high, the succession of natural species progressed more slowly, so that they could only settle to a greater extent later. As a result, diversity was able to increase, even in the oldest age group studied.

In the case of arable land, the diversity values were fluctuating but, overall, showed an upward trend similarly to other studies [47,48,55]. There was also an increase (6–10 years), a decrease (11–20 years), and then an increase in age group 4 (21–30 years). Contrary to the experience of Tatoni and Roche [57] and Debussche et al. [58], diversity did not show a declining trend from the 20th year onwards, but earlier (11–20 years). Our results partially support the experience of Molnár and Botta-Dukát [50] and Monk [59] that diversity did not change linearly during succession. The initial increase was probably due to newly introduced species, mostly weeds or weed-like species. With the extinction of these and the increase in the dominance of the remaining species, the diversity may have decreased, and then the settlement of the natural and more sensitive species in the oldest abandoned lands

(age group 4) may have caused the increase in diversity. The diversity of abandoned areas was, in any case, influenced by the cover of species with strong competitive capacity [40,47].

In abandoned grasslands, diversity decreased (age groups 2 and 3), and then increased slightly (age group 4), so it did not change linearly during succession, similar to Belsky's [92] experience. The declining diversity of abandoned grasslands confirms that the diversity of both extensive mowing and extensive grazing can be considered a maintenance treatment—see, e.g., Refs. [93–95].

In terms of average diversity, grasslands were the most diverse in the first 5 years after abandonment, while the diversity of vineyards were the lowest (Figure 3). In the case of the oldest fallows, the order was reversed between them, and the average value of the vineyards was higher for the Shannon diversity and the Simpson diversity, compared to the previous pastures/meadows. When looking at abandoned lands from different cultivations, the initial (age group 1) diversity values were very different but, after 30 years, these values gradually became similar.

4.3. Naturalness

The high proportion of ruderal competitors (RC) in the first two age groups of vineyards (Figure 4) can be explained by the high cover value of *Calamagrostis epigeios*, which has been present in the majority of vineyards since the first years. The former is not a unique phenomenon, as *Calamagrostis* may become abundant in the vineyards a few years after abandonment [71,73,90]. The increase in the rate of disturbance-tolerant species (DT) in the 11–20 age group is due to only two plant species (*Rubus caesius, Bothriocvloa ischemum*). Generalists became dominant only in the oldest abandoned lands, in contrast to vineyards in a similar landscape, where generalist species predominated in the 1–40 age group [17]. The presence and growth of sensitive species (a total of six species with an average cover value between 0.16% and 1.7%) in older fallows indicates regeneration.

The high proportion of ruderal competitors (RC) in the first three age groups of arable land (Figure 4) can be explained by the cover values of *Calamagrostis epigeios* and *Agropyron repens*, which have been present in the majority of arable land since the first years, and then predominant, similar to vineyards. The subdominant nature of competitor species (C) and the presence of specialists (S) (a total of six species with an average cover value between 0.08% and 0.5%) also support the increase in the number of species in natural and semi-natural habitats [48]. As semi-natural vegetation was present in small patches in the vicinity of the fallows, competitor species (C) became subdominant on the oldest plots, in addition to the generalist species—compare [50,65–68]. In grasslands, the increasing share of competitors (C) with abandonment time (Figure 4) is also confirmed by other research [38]. The specialist species were represented by a total of 11 species, with an average cover value between 0.01% and 5.73%.

Taking into account all the forms of social behavior types, it can be said that the studied abandoned grasslands became even more natural over time, i.e., they regenerated well.

4.4. Life Forms

In abandoned vineyards, the dominance of hemicryptophytes (H, e.g., *Calamagrostis epigeios, Elymus repens*) in the youngest fallow stands (Figure 5) is in contrast to the observations of others [2,72,90], where the share of therophytes was found to be the highest. In addition to the quality of the propagule pool, this difference was also due to the history of the landscape, the way of viticulture, and the relatively small size of the vineyards. The perennial grasses already appeared in the vineyards during the cultivation period [2], mainly from the adjacent plots. Woody microphanerophytes (M) already appeared here in the first years of succession and can even be found in all age groups [2,57,69,70].

In arable old-fields, a significant decrease in the number of annuals (Th) after a few years was also confirmed [5]. Woody microphanerophytes (M) occurred almost only in the oldest (age group 4) old-fields, a result that fits well into the so-called dominance order observed in old-field successions [57,59,61–63]. Other observations, however, suggest

that the number of woody species varied from age to age and appeared as early as the beginning of the succession [1,64]. Overall, hemicryptopyte species (H) became absolutely dominant in arable land 20 years after abandonment, with minimal but above 1% coverage of chamaepyte species (Ch).

The presence and high proportion of hemicryptopyte (H) species in abandoned grasslands (Figure 5) can be mainly explained by the dominance of perennial grasses and dicots, confirming the favorableness of abandonment for them—compare [43–45,96].

4.5. Multivariate Analysis

Regarding the arrangement, it can be said that, along the x-axis (the first principal component), mainly two species', Calamagrostis epigeios and Brachypodium rupeste, participation and dominance are dominant, while, along the y-axis, the condition and domination of *Elymus repens* and *Erigeron annuus* are decisive mainly (Figure 6). In the largest group in the far left of the figure, *Calamagrostis* (37–40%) is monodominant. *Brachypodium* reaches a maximum coverage of 6.1%. In the group of grapes aged 1–5 years, *Elymus repens* has a significant share (12%) and can be considered subdominant. In the smaller group on the right side of the figure, the cover of Brachypodium is high, the cover of Festuca rupicola may be significant (13%), while *Calamagrostis* is not present. The group observed in the lower part of the figure shows the values of the arable land aged 1–5 years, where *Elymus repens* (30%) is dominant, but the cover of *Erigeron annuus* is also significant (17%). The image is more varied in the case of values of abandoned plots closer to the intersection of the x and y axes; other species are also more pronounced. On the left side of the y-axis, Calamagrostis is still dominant in samples of arable lands abandoned for 6–10 and 21–30 years and vineyards abandoned for 21-30 years, and Inula ensifolia and Brachypodium rupestre cover values are significant (7% and 9%, respectively), while *Fragaria viridis* is a subdominant species in abandoned arable lands. Calamagrostis is predominant for samples 1–5 and 6–10-year-old grasslands to the right of the y-axis, with *Brachypodium* and *Festuca* being subdominant, or the latter two species codominant and *Calamagrostis* subdominant.

The lesser mixing between the groups of the investigated cultivation branches (vineyards, arable lands) reveals that, in the same landscape, the process of secondary succession of formerly differently cultivated areas is not sharply separated. The smaller size of the plots and the vegetation of the adjacent plots may also have played an important role in the background of the latter phenomenon. Succession processes may have accelerated in some places due to the contact of the abandoned lands at different stages of succession. Young abandoned fields had fewer weeds in the first years, and ruderal or perennial, possibly close-to-nature species may have appeared earlier [48,56,71,73,90]. However, due to the above mentioned, the succession path may be stuck on középidős older plots, e.g., due to the dominance of *Calamagrostis* [48,56,90]. The latter species can be replaced much more slowly by other natural species due to its strong root competition and lack of mowing [72].

5. Conclusions

The process of secondary succession of abandoned land from different cultivations (vineyards and arable plots) from the same landscape was not sharply separated from each other, but showed similarities based on several examined parameters. The total species richness and diversity of abandoned vineyards and arable land did not increase linearly in the four age groups studied. In these types, rapid regeneration of natural vegetation can be observed, the rate of which can only be reduced by the abundance of a few strong competitor species. The total species number of the youngest and oldest stands in the abandoned arable and vineyard plots was very similar. Among the youngest age groups of the studied types, the diversity values were still very different, but, after more than two decades, they became very similar. For all three types of abandonment studied, the number of life forms increased in the third decade after abandonment. This phenomenon can be well explained by changes in the species composition and diversity of vineyards and arable

lands. In the case of abandoned grasslands, textural and structural changes following the abandonment of mowing and grazing have led to an increase in the number of life forms.

The emergence and subsequent increase in the proportion of competitor (C) and specialist (S) species, as well as the decline in weed (W), disturbance-tolerant (DT), and alien competitor (AC) species, result in a favorable species composition for abandoned vineyards and arable land. The changes indicate that the colonization of certain steppe and forest-steppe species (e.g., *Festuca rupicola, Brachypodium rupestre*) may become stronger in the future. The change in naturalness over time indicates that, for vineyards and arable land, the distribution of each SBT category has become more balanced for the third decade of abandonment compared to the initial period, while, for grasslands, the opposite has been observed.

Abandonment of extensively grazed or mowed grasslands has decreased species numbers and diversity, which may reduce the resilience of such grasslands to environmental factors. In the latter habitats, therefore, abandonment of treatment has a negative effect on the composition of vegetation, in contrast to vineyards and arable land. In the case of abandoned lands, the rate of secondary succession and regeneration appear to be favored by the mosaic landscape and the previous extensive small-plot farming. The boundaries, orchards, and vegetation patches around old seed trees between the parcels and the edges have well preserved the species of the natural flora, including the forest-steppe and steppe species [76]. The propagation of the propagules of the latter species from the abovementioned refuges may have started after the end of cultivation, which was reflected in the increase in both the total species richness and the diversity values.

In the first 3 decades after the abandonment, the way of secondary succession of the studied arable land and vineyards may have been more strongly influenced not by the previous cultivation method, but by the same landscape, the species composition of the adjacent plots and edges, and the smaller size of the plots. It seems that the spontaneous succession is more effective when the species of natural grasslands are able to colonize at the very beginning of the succession from the nearby propagule pool. Based on our study, it can be said that, on plots abandoned from different cultivations, the spontaneous succession can be a sufficient way in the recovery of semi-natural grasslands in a diverse landscape.

Author Contributions: Conceptualization, O.S. and S.C.; methodology, S.C.; software, D.S.; formal analysis, D.S.; investigation, O.S. and S.C.; data curation, O.S.; writing—original draft preparation, O.S., D.S., L.K.B. and S.C.; writing—review and editing, O.S., D.S., L.K.B. and S.C.; visualization, O.S., D.S. and S.C.; supervision, S.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: The data that support the findings of this study are available on request from the corresponding author.

Acknowledgments: The research was supported by the Doctoral School of Environmental Sciences of the Szent István University and Ferenc Deák scholarship of the Ministry of Education and Culture (Hungary). We are grateful to Emily Hryb for the English language and style corrections, and for Károly Penksza and OTKA K-125423.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

		Vin	eyards			Arabl	e Land			Gra	sslands	
Species/Years after Abandonment	1–5	6–10	11-20	21-30	1–5	6–10	11–20	21–30	1–5	6–10	11-20	21–30
A/1												
Achillea collina	0.07	0.07	0.10	0.08	0.07	0.69	0.41	0.14	0.79	0.15	0.88	0.64
Achillea pannonica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.08	0.01	0.00
Agrimonia eupatoria	0.02	0.03	0.07	0.03	0.00	0.01	0.07	0.07	0.50	0.00	0.07	0.00
Alopecurus pratensis Anagallis arvensis	$0.17 \\ 0.00$	0.00 0.03	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$0.00 \\ 0.01$	$\begin{array}{c} 0.00\\ 0.00\end{array}$	$0.00 \\ 0.00$	$0.01 \\ 0.00$	$1.75 \\ 0.00$	$\begin{array}{c} 0.14 \\ 0.00 \end{array}$	$0.00 \\ 0.00$	$0.00 \\ 0.00$
Anemone sylvestris	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.63
Anthoxanthum odoratum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	2.01	0.07	0.00	0.00
Arrhenatherum elatius	0.00	0.24	0.45	0.36	0.00	0.57	0.11	2.53	11.88	5.53	0.01	0.44
Artemisia campestris	$0.00 \\ 0.03$	$0.00 \\ 0.00$	$1.03 \\ 0.04$	$0.00 \\ 0.00$	$0.00 \\ 0.01$	$0.00 \\ 0.07$	$0.00 \\ 0.27$	$0.00 \\ 0.00$	$0.00 \\ 0.01$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.00 \\ 0.00$	$\begin{array}{c} 0.00\\ 0.00\end{array}$
Artemisia vulgaris Asperula cynanchica	0.03	0.00	0.04	0.00	0.01	0.07	0.27	0.00	0.01	0.00	0.00	1.94
Aster amellus	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aster linosyris	0.00	0.00	1.64	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.44
Astragalus cicer	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00
Astragalus glycyphyllos Avenula pratensis	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.00 \\ 0.00$	0.02 0.00	$0.00 \\ 0.16$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.00 \\ 0.00$	$0.00 \\ 0.00$	0.13 0.00	$0.13 \\ 0.00$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	0.20 0.00	$1.82 \\ 0.00$
Avenula pubescens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.33	0.47	0.00
Betonica officinalis	0.17	2.67	0.00	0.10	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.33
Botriochloa ischaemum	0.00	0.00	8.30	1.30	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.00
Brachypodium rupestre Briza media	$0.00 \\ 0.00$	2.67 0.00	$6.14 \\ 0.00$	6.90 0.09	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	0.56 0.02	0.00 1.23	$1.00 \\ 0.35$	13.44 0.70	$6.67 \\ 0.08$	43.33 1.03	43.94 0.01
Bromus inermis	0.00	1.07	0.00	0.09	0.00	2.22	0.00	0.00	0.00	0.08	0.00	0.01
Bromus sterilis	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buglossoides arvensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00
Buglossoides purpureo-c. Calamagrostis epigeios	$0.00 \\ 48.17$	$0.00 \\ 43.20$	$0.00 \\ 42.69$	$0.00 \\ 22.15$	$0.00 \\ 2.50$	$0.00 \\ 24.72$	0.00 37.29	0.00 21.53	$0.00 \\ 8.07$	$0.00 \\ 13.00$	$0.00 \\ 0.00$	$0.00 \\ 0.00$
Campanula glomerata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Campanula patula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00
Campanula sibirica	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.01
Campanula sp. Carduus nutans	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.01 \\ 0.00$	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$\begin{array}{c} 0.00\\ 0.00 \end{array}$	$0.00 \\ 0.01$	$0.00 \\ 0.00$	$0.00 \\ 0.08$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.00 \\ 0.00$	$0.00 \\ 0.00$
Carex humilis	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Carex montana	0.00	0.00	0.18	0.88	0.00	0.17	0.00	0.33	1.88	2.00	0.00	1.69
Carex praecox	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00
Carex stenophylla Carex tomentosa	$0.00 \\ 0.00$	0.00 0.00	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$\begin{array}{c} 0.00\\ 0.00 \end{array}$	$0.00 \\ 0.00$	$0.00 \\ 0.67$	$0.00 \\ 0.03$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	0.00 0.02	0.01 0.02
Carlina vulgaris	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Centaurea jacea	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.07	0.00	0.00	0.00	0.00
Centaurea pannonica	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	3.50	0.01	0.00	0.00
Centaurea scabiosa Centaurium minus	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$1.60 \\ 0.00$	$0.17 \\ 0.00$	$0.09 \\ 0.00$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$\begin{array}{c} 0.00\\ 0.00\end{array}$	0.29 0.01	0.07 0.01	$0.00 \\ 0.00$	$0.00 \\ 0.01$	0.99 0.00	$3.51 \\ 0.00$
Cerastium fontanum	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.00	0.00
Chamaecytisus albus	0.00	0.00	2.23	0.10	0.00	0.00	0.00	0.00	0.00	0.00	3.20	0.00
Chondrilla juncea	0.00	0.07	0.02	0.07	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00
Chrysopogon gryllus Cirsium arvense	$0.00 \\ 0.80$	$0.00 \\ 0.31$	$0.00 \\ 0.16$	0.00 0.02	0.00 3.36	$\begin{array}{c} 0.11 \\ 0.44 \end{array}$	$0.00 \\ 0.11$	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	1.73 0.03	$0.00 \\ 0.00$
Cirsium eriophorum	0.00	0.00	0.10	0.02	0.00	0.00	0.04	0.00	1.56	0.37	0.00	0.00
Cirsium pannonicum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26
Clematis recta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.81
A/2												
Clematis vitalba	0.10	0.00	0.18	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Colchicum autumnale	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Colutea arborescens Convolvulus arvensis	$0.00 \\ 0.09$	$0.00 \\ 0.15$	$0.03 \\ 0.04$	$0.00 \\ 0.09$	$0.00 \\ 0.67$	$0.00 \\ 0.56$	$0.00 \\ 0.15$	0.03 0.01	$0.00 \\ 0.19$	$0.00 \\ 0.02$	$0.00 \\ 0.01$	$0.00 \\ 0.94$
Conyza canadensis	0.09	0.13	0.04	0.09	6.89	0.00	0.13	0.01	0.19	0.02	0.01	0.04
Cornus sanguinea	0.03	0.00	1.29	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coronilla varia	0.00	0.57	0.68	0.14	0.13	0.00	0.21	1.47	0.00	0.33	0.14	2.25
Crataegus monogyna Crataegus oxyacantha	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$\begin{array}{c} 0.00\\ 0.00 \end{array}$	$0.00 \\ 0.00$	$0.00 \\ 0.00$	$0.01 \\ 0.00$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.00 \\ 0.00$	0.06 0.13
Crepis biennis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Crepis praemorsa	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cruciata glabra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01
Dactylis glomerata Daucus carota	1.67 0.08	2.21 1.94	3.14 0.00	0.69 0.00	0.94 0.32	5.32 0.23	$0.01 \\ 0.09$	0.11 0.02	9.26 0.00	$4.60 \\ 0.01$	0.02 0.01	0.02 0.00
Dianthus pontederae	0.00	0.00	0.00	0.00	0.00	0.25	0.09	0.02	0.00	0.01	0.01	0.00
Dipsacus laciniatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00
Doronicum hungaricum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Dorycnium herbaceum Dorycnium sp.	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	1.37 0.00	0.03 0.00	0.57 2.50	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$\begin{array}{c} 0.00\\ 0.00\end{array}$	$2.14 \\ 0.00$	$0.00 \\ 0.00$	0.03 0.00	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.00 \\ 3.00$	0.50 1.25
Echinochloa crus-galli	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echium maculatum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.13

 Table A1. Coenological data (average) of land use types and abandonment categories.

 Table A1. Cont.

		Vineyards Arable Land						Gras	Grasslands			
Species/Years after Abandonment	1–5	6–10	11-20	21–30	1–5	6–10	11-20	21–30	1–5	6–10	11–20	21–30
Elymus hispidus	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Elymus repens Freilebium parsiflanoum	12.67	5.17	0.33	0.00	30.00	2.50	0.00	0.00	0.00	3.67	0.00	0.00
Epilobium parvifloroum	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Erigeron annuus Erigeron campactra	$1.45 \\ 0.00$	$1.64 \\ 0.00$	$\begin{array}{c} 0.11 \\ 0.00 \end{array}$	0.10 0.27	$17.28 \\ 0.00$	1.34 0.01	$0.79 \\ 0.14$	$\begin{array}{c} 0.01 \\ 0.00 \end{array}$	$0.01 \\ 0.00$	$0.00 \\ 0.00$	$0.00 \\ 0.93$	$0.00 \\ 1.08$
Eryngium campestre Euonymus verrucosus	0.00	0.00	0.00	0.27	0.00	0.01	0.14	0.00	0.00	0.00	0.93	0.00
Euphorbia cyparissias	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Euphorbia cypurissius Euphorbia polychroma	0.00	0.01	0.04	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.02	0.15
Euphorbia salicifolia	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Euphorbia virgata	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.11	0.00	0.03
Falcaria vulgaris	0.03	0.34	0.02	0.00	0.01	0.00	4.07	0.31	0.00	0.80	0.07	0.14
Festuca javorkae	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Festuca pratensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.87	0.01	0.00
Festuca pseudovina	0.00	0.00	0.21	0.00	0.01	1.28	10.36	4.67	0.00	0.33	0.00	0.00
Festuca rupicola	0.00	0.67	0.00	1.94	0.00	5.89	0.00	10.00	15.94	9.67	13.87	1.58
Festuca valesiaca	0.00	0.00	1.71	2.05	0.00	0.13	0.14	6.67	3.13	6.00	3.74	0.00
Festuca $ imes$ wagneri	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Filipendula vulgaris	0.00	0.00	0.00	0.31	0.00	0.28	0.04	1.94	1.48	0.20	1.29	0.88
Fragaria viridis	0.00	1.93	1.25	0.04	0.25	13.29	16.79	14.37	4.06	0.81	0.22	0.38
Fragaria $ imes$ ananassa	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galinsoga parviflora	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galium mollugo	0.00	0.00	0.03	1.47	0.00	0.00	0.14	0.21	1.66	0.60	0.00	0.00
Galium rubioides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.13	0.00	0.00	0.00
Galium verum	0.00	0.00	0.07	0.00	0.00	0.00	0.08	0.57	5.50	5.53	0.15	0.00
Geranium sanguineum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Glechoma hederacea	0.07	0.03	0.00	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Helianthemum ovatum	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.26
Heracleum sphondylium	0.27	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.19	0.07	0.00	0.00
Iieracium bauhinii	0.02	0.16	0.13	0.49	0.00	0.44	2.99	0.07	0.00	0.00	0.00	0.00
Hieracium cymosum	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4/3	0.00	0.07	0.00	0.02	0.01	0.00	0.00	1 (17	0.00	0.01	0.00	0.01
Hieracium pilosella	0.00	0.07	0.00	0.02	0.31	0.00	0.00	1.67	0.00	0.01	0.00	0.01
Hieracium umbellatum	0.00	0.07	0.01	0.00	0.01	0.00	0.36	0.28	0.00	0.01	0.00	0.00
Hypericum perforatum	0.00	0.05	0.00	0.00	0.00	0.00	0.14	0.17	0.16	0.08	0.00	0.00
Hypochoeris maculata	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00
Inula britannica	0.00	0.12	0.35	5.28	0.31	3.01	0.16	0.01	0.13	0.00	1.00	0.38
Inula ensifolia	0.00	1.17	0.37	9.29	0.00	0.00	0.64	3.33	0.00	1.54	0.14	1.38
Inula hirta	$\begin{array}{c} 0.00\\ 0.00\end{array}$	$\begin{array}{c} 0.00 \\ 0.00 \end{array}$	$0.00 \\ 0.02$	$0.00 \\ 1.13$	$0.00 \\ 0.00$	$\begin{array}{c} 0.01 \\ 0.00 \end{array}$	$0.00 \\ 6.15$	$0.01 \\ 16.00$	0.00 0.03	$0.00 \\ 0.00$	$0.00 \\ 0.00$	0.00
Inula salicina Iris variegata	0.00	0.00	0.02	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00
Knautia arvensis	0.00	0.00	0.00	0.00	0.00	0.00	1.76	0.40	1.51	2.37	0.00	0.00
Koeleria cristata	0.00	1.04	1.27	0.53	0.00	1.56	0.86	0.40	0.00	0.00	0.00	0.60
Lactuca sativa	0.00	0.00	0.00	0.00	1.88	0.00	0.00	0.00	0.00	0.00	0.20	0.00
Lamium purpureum	0.00	0.00	0.00	0.00	0.00	2.22	0.00	0.00	0.00	0.00	0.00	0.00
Lathyrus lathifolius	0.01	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lathyrus niger	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lathyrus pratensis	0.00	0.00	0.00	0.78	0.00	0.00	1.89	0.00	4.25	0.02	0.00	0.00
Lathyrus tuberosus	0.04	0.23	0.04	0.11	0.58	2.41	1.79	0.17	0.13	0.00	0.00	0.00
Lembotropis nigricans	0.00	0.00	0.00	0.70	0.00	0.00	0.00	0.00	0.00	0.53	0.01	0.32
Leontodon autumnalis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Leontodon hispidus	0.03	0.13	0.00	0.00	0.00	0.06	0.57	1.14	0.84	1.61	0.00	0.00
Lepidium draba	0.27	0.41	0.00	0.00	0.00	0.28	0.11	0.03	0.00	0.10	0.00	0.00
Lepidium ruderale	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00
eucanthemum vulgare ssp. v.	0.00	0.00	0.00	0.00	0.00	0.11	0.09	0.01	0.13	0.00	0.01	0.00
libanotis pyrenaica	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ligustrum vulgare	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Linaria vulgaris	0.03	0.01	0.00	0.10	0.21	0.02	0.02	0.00	0.00	0.00	0.00	0.00
Linum flavum	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
inum tenuifolium	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lotus corniculatus	0.00	0.00	0.00	0.32	0.00	0.01	2.11	0.27	0.51	0.00	0.14	0.00
uzula campestris	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.04	0.00	0.00	0.00
ychnis viscaria	0.10	0.03	0.12	0.03	0.00	0.11	0.09	0.11	0.11	0.00	0.00	0.00
ysimachia nummularia	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Ňedicago falcata	0.00	0.00	0.00	0.00	0.06	0.17	0.00	0.00	0.00	0.34	3.47	3.13
Medicago sativa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.01
Melilotus officinalis	0.00	1.45	0.20	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Minuartia setacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Muscari comosum	0.00	0.02	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.01
Myosotis arvensis	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nonea pulla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Onobrychis arenaria	0.00	0.00	0.70	0.63	0.00	0.00	0.00	0.00	0.00	0.00	3.54	2.19
Ononis spinosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.19	0.23	0.00	0.00
Driganum vulgare	0.00	0.03	0.02	0.08	0.06	0.00	0.07	0.00	0.13	0.00	0.00	0.19
Oxalis dillenii	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peucedanum alsaticum	0.64	0.07	0.18	1.02	0.01	0.45	0.59	0.21	0.56	0.61	0.00	0.06

Table A1. Cont.

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 | | Vin | eyards |
 | | Arabl | e Land |
 | Grasslands | | |
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Species/Years after Abandonment			

 | 1–5 | 6–10 | 11–20 | 21–30
 | 1–5 | 6–10 | 11-20 | 21–30
 | 1–5 | 6–10 | 11–20 | 21-30
 |
| Phleum phleoides
Picris hieracioides
Pimpinella saxifraga
Plantago lanceolata
Plantago major
Plantago media

 | $\begin{array}{c} 0.00 \\ 0.41 \\ 0.00 \\ 0.00 \\ 0.01 \\ 0.03 \end{array}$ | $\begin{array}{c} 0.00\\ 0.81\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ \end{array}$ | $\begin{array}{c} 0.00\\ 0.11\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ \end{array}$ | $\begin{array}{c} 0.00\\ 0.11\\ 0.27\\ 0.00\\ 0.00\\ 0.05 \end{array}$
 | $\begin{array}{c} 0.00 \\ 4.44 \\ 0.00 \\ 0.38 \\ 0.08 \\ 0.08 \end{array}$ | $\begin{array}{c} 0.00 \\ 0.06 \\ 0.01 \\ 0.28 \\ 0.00 \\ 0.23 \end{array}$ | $\begin{array}{c} 0.00 \\ 0.72 \\ 0.00 \\ 0.08 \\ 0.00 \\ 3.51 \end{array}$ | $\begin{array}{c} 0.00 \\ 0.00 \\ 0.20 \\ 0.03 \\ 0.00 \\ 2.91 \end{array}$
 | $\begin{array}{c} 0.00 \\ 0.00 \\ 1.01 \\ 0.00 \\ 0.00 \\ 0.16 \end{array}$ | $\begin{array}{c} 0.00\\ 0.01\\ 0.13\\ 0.07\\ 0.00\\ 0.53\end{array}$ | $\begin{array}{c} 0.87 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.15 \end{array}$ | $\begin{array}{c} 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.07 \end{array}$
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| A/4

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| AV4 Poa angustifolia Poa pratensis Polygala comosa Polygala major Polygala major Polygonum lapathifolium Potentilla alba Potentilla argentea Prunella grandiflora Prunella vulgaris Prunus domestica Prunus domestica Prunus spinosa Pseudolysimachion spicatum Pulmonaria mollis Pulstilla grandis Pyrus pyraster Quercus robur Ranunculus acris Ranunculus arvensis Ranunculus arvensis Ranunculus polyanthemos Rapistrum perenne Reseda lutea Rhinanthus rumelicus Robinia pseudo-acacia Rosa sp. Rubus coryllifolius Rumex acetosa Salvia austriaca Salvia pratensis Salvia pratensis Salvia verticillata Sanguisorba minor Sedum maximum Sedum sexangulare Senecio erucifolius Senecio acoia Serrai pumila </td <td>0.00
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| Solidago canadensis
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| Solidago virga-aurea
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Stachys recta
Stellaria graminea
Stipa pulcherrima
Symphytum officinale
Symphytum tuberosum
Tanacetum corymbosum
Tanacetum vulgare
Taraxacum officinale
Teucrium chamaedrys
Thesium linophyllon
Thymus glabrescens
Thymus pannonicus
Tragopogon orientalis
Trifolium alpestre

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 | $\begin{array}{c} 0.01\\ 0.00\\ 0.00\\ 0.00\\ 1.63\\ 0.00\\ 0.88\\ 0.00\\$ | $\begin{array}{c} 0.00\\ 0.06\\ 0.00\\$ | $\begin{array}{c} 0.76 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 4.29 \end{array}$ | $\begin{array}{c} 0.12\\ 0.00\\ 0.00\\ 0.34\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.13\\ 0.00\\ 2.13\\ 0.00\\ 0.07\\ \end{array}$
 | $\begin{array}{c} 0.00\\ 0.00\\ 0.00\\ 0.76\\ 0.00\\ 0.06\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 1.19\\ 1.14\\ 0.01\\ 0.00\\ 0.25\\ \end{array}$ | $\begin{array}{c} 0.27\\ 0.00\\ 0.03\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.01\\ 0.00\\ 0.01\\ 0.00\\ 0.01\\ 0.00\\ 0.00\\ 0.07\\ \end{array}$ | $\begin{array}{c} 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.07\\ 0.01\\ 0.00\\ 2.07\\ 0.22\\ 0.67\\ 0.00\\ 0.01\\ 1.34 \end{array}$ | $\begin{array}{c} 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 1.82\\ 0.01\\ 0.00\\ 0.00\\ 0.00\\ 0.00\\ 9.13 \end{array}$
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		Vin	eyards		Arable Land					Grasslands					
Species/Years after Abandonment	1–5	6–10	11–20	21–30	1–5	6–10	11–20	21–30	1–5	6–10	11–20	21–30			
Trifolium arvense	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.07	0.00	0.00			
Trifolium campestre	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00			
Trifolium montanum	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.20	0.69	0.00	0.61	2.81			
Trifolium pratense	0.00	0.00	0.00	0.00	0.06	2.84	0.16	0.13	0.20	0.00	0.53	0.63			
Trifolium repens	0.00	0.00	0.00	0.00	0.33	0.11	0.00	0.00	0.00	0.00	0.00	0.00			
Trifolium rubens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.00	0.00	0.00			
Trisetum flavescens	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.07	0.64	0.81	0.00	0.00			
Tussilago farfara	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
Ulmus minor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50			
Valeriana officinalis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13			
Verbascum austriacum	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00			
Verbascum lychnitis	0.00	0.10	0.00	0.02	0.00	0.00	0.00	0.13	0.50	0.20	0.00	0.00			
Verbascum phoeniceum	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.08			
Veronica chamaedrys	0.00	0.02	0.00	0.01	0.01	0.00	0.16	0.11	0.03	0.05	0.00	0.00			
Vicia cracca	0.13	0.93	0.02	0.08	0.00	0.06	0.21	0.01	1.25	16.40	0.00	0.88			
Vicia tetrasperma	0.00	0.00	0.00	0.00	0.13	0.01	0.33	0.03	0.06	0.07	0.00	0.00			
Vinca minor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00			
Vincetoxicum hirundinaria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13			
Viola canina	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00			
Viola elatior	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00			
Viola hirta	0.02	0.07	0.03	0.07	0.00	0.00	0.00	0.01	0.00	0.20	0.07	0.31			
Viola kitaibeliana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
Viola sylvestris	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
Vitis vinifera	8.53	3.37	4.11	0.79	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00			
Zea mays	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00			

Table A1. Cont.

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